UNIFORMITY OF SUCCESSIVE POPULATIONS OF AN ALPINE GRASSHOPPER WITH A TWO-YEAR DIAPAUSE[1]

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While studying the life history of *Aeropedellus clavatus* (Thomas) in the alpine tundra of Colorado, John Hilliard and I found that the life cycle at high altitudes involves two winters in the egg stage, a two-year embryonic diapause (Alexander & Hilliard, 1964). This is not an exceptional pattern for boreal Orthoptera (Criddle, 1933; Pickford, 1953), though it had not been previously reported for this species. Eggs from populations of *A. clavatus* at lower altitudes in Colorado, in contrast, hatch after only one winter in the egg stage. This difference in the life cycles raises the question: Are samples from successive years in the same alpine area essentially uniform?

One assumes that samples from successive years in an area at lower altitude are uniform because they are derived from the same gene pool. Presumably, however, one cannot make the same assumption in an apline area; there could be, conceivably, two different gene pools, and these could be related to two morphologically distinct groups. If there are two distinct groups, characterizations of alpine populations, which up to now have assumed relative uniformity in all samples from a given locality (Alexander, 1961), must take this into account.

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To determine whether or not samples from successive years at the same locality are essentially uniform we must examine samples from several successive years. Large samples from a long series of years would be desirable, but I know of no extensive collections in single alpine localities for more than three successive years. It seems desirable, therefore, to use what is available–rather large samples from three successive years at three different locations on Mount Evans, Colorado.

My associates and I made large collections of *A. clavatus* in 1958, 1959, and 1960 at three different collecting stations above tree line on Mount Evans: 1. Near Goliath Peak, at 12,100 ft. (3,690 m.) altitude. 2. At Summit Lake, altitude 12,800 ft. (3,900 m.) 3. At the "Upper Saddle," altitude 13,100 ft. (4,000 m). These specimens were available for the present study. (For descriptions of the localities see Alexander & Hilliard, 1969).

Only adult males were used in this analysis because the morphological differences we have found so striking in contrasting alpine populations are more conspicuous in males than in females. Further, the specimens used were those only in which all measurements could be made on each individual. In other words, a specimen too badly damaged for all measurements (e.g., a specimen without either antenna) was excluded from the samples. Even with these restrictions fairly large samples were available for all three years from Summit Lake and the Upper Saddle and moderately large samples from Goliath Peak.

Striking morphological variations between alpine populations of *A. clavatus* occur, the differences so conspicuous at times that one can distinguish at sight between specimens from two different localities. Differences in size distinguish some populations, but the most conspicuous differences often involve the shapes of the prothoracic tibiae and the antennal "knobs." All specimens from some populations have swollen anterior tibiae; in other populations these tibiae are relatively narrow. In some populations all specimens have conspicuously terminal antennal segments; in other populations the antennal "knobs" are relatively narrow.

Although all individuals from Mount Evans populations have swollen tibiae and broad antennal "knobs" it seemed likely that slight but consistent differences in the proportions–or in body dimensions–might, if they exist, be statistically detectable.

(Actually, there are significant differences between populations in the present study.) And so the present study was undertaken to determine if statistically significant differences occur between samples from successive years at the same locality.

Five measurements or sets of measurements were taken on each specimen. These were total length, length of pronotum, length of hind femur, and measurements to determine ratios of width to length of anterior tibia and seven distal antennal segments. (For measurements to determine ratios see Figure 1.) I studied tegminal length in these samples but abandoned using it as a statistic because of the difficulty of determining the location of the proximal end–variously exposed or concealed, depending upon mounting technique.

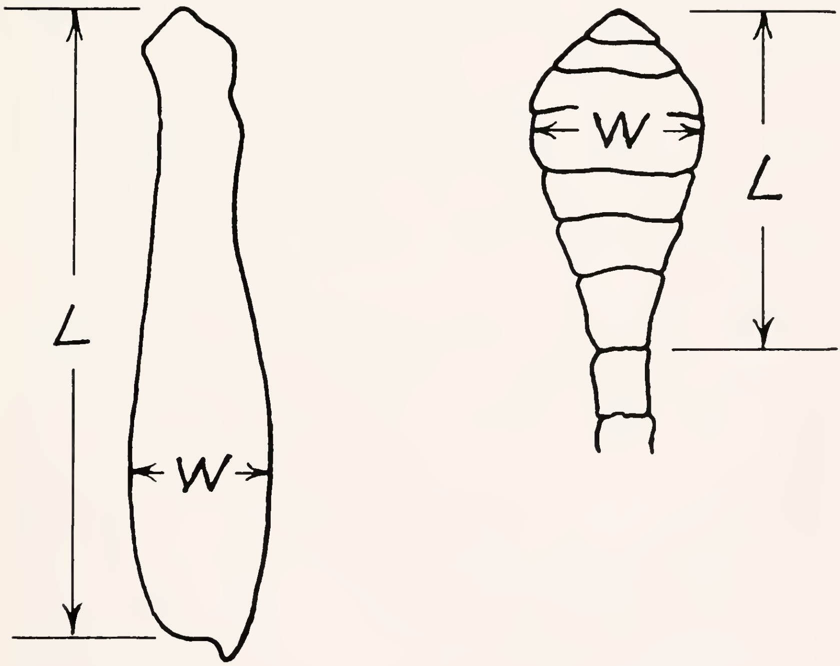

Figure 1. Dimensions used in calculating L/W ratios for prothoracic tibia (left) and distal seven antennal segments (right). The tibia was measured as seen in front, the antenna at its widest expanse. The drawings are of Summit Lake specimens in which the tibial ratio was 4.5, the antennal ratio, 1.9.

Measurements were made under a dissecting binocular, using a carefully calibrated reticule, the stated magnifications being X7 for total length, X10 for femur, X20 for pronotum and tibia, X25 for antennal segments. Dimensions (in millimeters) and ratios were rounded to the nearest 0.1.

Femur length was the most consistent indicator of size, this dimension showing a very low coefficient of variability. Pronotal length, surprisingly, had a generally higher coefficient of variability, though still within the range of average variability (Simpson, et al, 1960). Total length is of less value as a dimension, even with a relatively low coefficient of variability, because it varies more with age after the final molt and with mounting techniques. Both the ratios calculated were important for the present study, in spite of fairly high coefficients of variability in the antennal ratio. Variations in the antennal "knob" were, I believe, due more to modifications of the structure in drying than to natural variability.

I made no attempt to use color variations as these are not preserved in dried specimens. And of the internal genitalia, I examined only the epiphalli of a dozen specimens but found so much variation within a single sample that this offered less potential value for the study than the more obvious external features.

Results of the analysis of samples from the three localities appear in Tables I, II, and III. The numbers of data incorporated in these tables involved seven measurements each of 67 specimens from Goliath Peak, 120 from Summit Lake, and 92 from the Upper Saddle, nearly 2,000 measurements in all.

If significant differences distinguish successive populations at the same station sample values should indicate greater differences between samples from successive years than between samples two years apart. If such differences appear in this study, therefore, they should occur between samples from 1958 and 1959 and between those from 1959 and 1960. Samples collected at a given station in 1958 and 1960 should have essentially the same sample values. And if the statistical attributes of the 1959 sample do not clearly indicate differences in it from the 1958 and 1960 samples then we can assume that description of a population on the basis of a sample taken in a single year or in successive years is valid.

It is apparent, from examination of the tables, that the differences between two samples taken in successive years at the same station are no greater than the differences between samples from alternate years. Thus, in Table I (Goliath Peak population) we find the same mean values for femur length and tibial ratio in 1958 and 1959 and for pronotum length and antennal ratio in

TABLE I. Characteristics of samples from Goliath Peak population, at 3,690 m. altitude. Numbers in each sample were 18 (1958), 18 (1959), and 31 (1960), all adult males. Dimensions are in millimeters to the nearest 0.1 mm. The L/W ratios were obtained by using the measurements indicated in Figure 1 and were rounded to the nearest 0.1. The last four columns give means, standard deviations, atandard errors, and coefficients of variability, respectively.

	Year	Range	$\bar{X}$	s	$s/\sqrt{N}$	V
	'58	15.2 - 17.5	16.2	0.65	0.15	4.0
Total Length	'59	14.9 - 16.7	16.0	0.59	0.14	3.7
	'60	15.1 - 18.2	16.6	0.70	0.12	4.2
Length	'58	3.4 - 3.8	3.6	0.11	0.03	3.0
of	'59	3.1 - 3.8	3.5	0.22	0.05	6.3
Pronotum	'60	3.1 - 3.8	3.5	0.17	0.03	4.9
Length	'58	9.0 - 10.4	9.7	0.44	0.10	4.5
of	'59	8.6 - 10.1	9.7	0.41	0.10	4.2
Hind Femur	'60	8.9 - 10.5	9.8	0.41	0.07	4.2
Ratio L/W	'58	3.8 - 5.0	4.5	0.30	0.07	6.7
of	'59	4.1 - 5.0	4.5	0.28	0.07	6.2
Front Tibia	'60	4.1 - 5.3	4.6	0.31	0.05	6.7
Ratio L/W	'58	1.5 - 2.1	1.9	0.14	0.03	7.4
of	'59	1.5 - 2.1	1.8	0.15	0.04	8.3
Antennal "Knob"	'60	1.5 - 2.5	1.8	0.20	0.03	10.5

1959 and 1960. With total length we get a suggestion of a difference in successive years, but the 1958 and 1959 samples are more like each other than either is like the 1960 sample. In Table II (Summit Lake population) we find 1958 and 1960 mean values are the same for the other three statistics. In Table III (Upper Saddle population) means for the pronotum and antennal ratio are the same for all three years and the mean values for femur length are the same in 1959 and 1960. Only with total length and the tibial ratio is there a suggestion, a weak one, that the 1959 sample differs from the others (and in the case of the tibial ratio the figures were, before rounding to the nearest 0.1, 4.22, 4.15, and 4.16). When we consider ranges of values, standard deviations, and

TABLE II. Characteristics of samples from Summit Lake population, at 3,900 m. altitude. Numbers in each sample were 43 (1958), 41 (1959), and 36 (1960), all adult males. See Table I for other explanations.

	Year	Range	$\bar{X}$	s	$s/\sqrt{N}$	V
	'58	15.1 - 18.5	16.9	0.67	0.10	4.0
Total Length	'59	15.6 - 18.5	16.9	0.77	0.12	4.6
	'60	15.6 - 19.0	17.3	0.83	0.14	4.7
Length	'58	3.3 - 4.2	3.8	0.20	0.03	5.3
of	'59	3.3 - 4.0	3.8	0.27	0.04	7.1
Pronotum	'60	3.3 - 4.0	3.7	0.20	0.03	5.4
Length	'58	9.6 - 11.0	10.3	0.28	0.04	2.6
of	'59	9.4 - 11.1	10.2	0.33	0.05	3.2
Hind Femur	'60	9.0 - 11.4	10.2	0.50	0.08	4.9
Ratio L/W	'58	3.9 - 5.3	4.5	0.35	0.05	7.8
of	'59	3.9 - 5.3	4.4	0.30	0.05	6.8
Front Tibia	'60	4.0 - 5.1	4.4	0.28	0.05	6.4
Ratio L/W	'58	1.4 - 2.4	1.8	0.22	0.03	11.1
of	'59	1.5 - 2.4	1.9	0.20	0.03	10.5
Antennal "Knob"	'60	1.5 - 2.2	1.9	0.14	0.02	7.4

standard errors of the means, the differences that appear between means in the tables are really negligible.

These data clearly indicate that samples from three successive years at the same locality are essentially alike, and that the existence of what may usually be a two-year diapause does not produce genetic isolation between successive populations. There are two ways in which such a potential isolating mechanism could fail to operate. If some eggs from a high altitude population hatch during the year following laying—and this happened once in our experimentals—isolation would not be complete. This is not nearly so likely, however, as the possibility that diapause may extend

TABLE III. Characteristics of samples from Upper Saddle population, at 4,000 m. altitude. Numbers in each sample were 36 (1958), 24 (1959), and 32 (1960), all adult males. See Table I for other explanations.

	Year	Range	$\bar{X}$	s	$s/\sqrt{N}$	V
	'58	15.4 - 18.7	17.3	0.70	0.12	4.0
Total Length	'59	15.5 - 18.2	16.9	0.59	0.12	3.5
	'60	16.1 - 18.7	17.3	0.77	0.13	4.5
Length	'58	3.3 - 4.0	3.7	0.13	0.02	3.5
of	'59	3.4 - 4.0	3.7	0.14	0.02	3.8
Pronotum	'60	3.3 - 4.0	3.7	0.17	0.02	3.7
Length	'58	9.5 - 10.9	10.3	0.36	0.06	3.5
of	'59	9.6 - 10.6	10.1	0.30	0.06	3.0
Hind Femur	'60	9.5 - 10.7	10.1	0.31	0.05	3.1
Ratio L/W	'58	3.7 - 4.9	4.2	0.28	0.05	6.7
of	'59	3.7 - 4.6	4.1	0.22	0.04	5.4
Front Tibia	'60	3.7 - 4.7	4.2	0.24	0.04	5.7
Ratio L/W	'58	1.6 - 2.4	1.9	0.20	0.03	10.0
of	'59	1.5 - 2.3	1.9	0.17	0.03	8.9
Antennal "Knob"	'60	1.6 - 2.3	1.9	0.17	0.02	8.9

over three winters rather than two in many of the eggs, a condition already demonstrated as occurring in a sizable proportion of the eggs of several high altitude species tested by Kreasky (1960). It is this possibility, I believe, that assures us of a relatively uniform year-to-year gene pool in a tundra population.

My conclusion is, therefore, that we may safely characterize each alpine population of *A. clavatus* on Mount Evans by samples from a single year or successive years. And on the basis of this study, I believe we are justified in applying the same principle in characterizing other alpine populations of this species, using samples from either a single year or successive years.

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ABSTRACT:–UNIFORMITY OF SUCCESSIVE POPULATIONS OF AN ALPINE GRASSHOPPER WITH A TWO YEAR DIAPAUSE. *Aeropedellus clavatus* (Thomas), an abundant grasshopper in the alpine tundra of Colorado, has a two-year diapause. This suggests the possibility of two distinct populations in successive years. Statistical analysis of samples from three alpine localities on Mount Evans, Colorado, collected in 1958, 1959, and 1960, demonstrate that samples from successive years are as much alike as are those from 1958 and 1960. Successive populations are therefore essentially uniform. Apparently all individuals do not have a two-year diapause, a few eggs hatching after only one winter while a larger number, probably, go through three winters before hatching.–Gordon Alexander, 765 14th street, Boulder, CO 80302.

Descriptors: alpine, diapause, grasshopper, populations.